PRECOCIOUS MATURITY OF THE MAJID CRAB, *PUGETTIA PRODUCTA*, PARASITIZED BY THE RHIZOCEPHALAN BARNACLE, *HETEROSACCUS CALIFORNICUS*

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ABSTRACT

Mean size of adult kelp crabs, *Pugettia producta*, parasitized by the rhizocephalan barnacle, *Heterosaccus californicus*, was significantly less than the mean size of unparasitized crabs. This size difference resulted from parasitized animals having passed through fewer instars before the molt of puberty. Laboratory and field evidence indicated that parasitized crabs matured earlier than unparasitized ones. Precocious maturity of parasitized crabs fitted a model which postulated that size at maturity was determined by the value of a size-threshold. Crabs would not undergo the molt of puberty unless larger than the size-threshold. The value of the size-threshold would be influenced by environmental factors which could vary seasonally within one locality. Precocious maturity can be explained as a greater sensitivity of parasitized crabs to the stimuli that induce maturation above the size-threshold. The implication of this study is that size differences among populations of adult crustaceans may be accounted for by variation in the number of juvenile instars as well as size-selective predation and differential growth.

INTRODUCTION

The Rhizocephala are a distinctive order of barnacles which parasitize decapod crustaceans. In addition to inhibiting host reproduction and feminizing male hosts (see Hartnoll, 1967, for review), the parasite may affect adult host size. For example, Reinhard (1950, 1956) observed that *Callinectes sapidus* parasitized by mature *Loxothylacus texanus* were smaller than unparasitized adults and considered this to be due to hyperfeminization, a condition in which parasitized hosts precociously developed the broad adult female abdomen. Hartnoll (1967) termed this effect precocious maturity. Allen (1966) observed a similar phenomenon with another crustacean parasitic castrator, reporting that pandalid shrimp parasitized by a bopyrid isopod precociously developed breeding dress. A smaller mean size of parasitized hosts which may indicate precocious maturity has been noted for many sacculinid-host associations: Smith (1906), Okada and Miyashita (1935), Veillet (1945), Reinhard (1950), Overstreet (1978), and O'Brien (this study). In contrast, Philipps and Cannon (1978) reported no effect of a sacculinid on host size while Day (1935) and Vernet-Cornubert (1958) documented interactions in which sacculinid prevalence increased with increasing host size.

Interactions other than precocious maturity occur in other rhizocephalan families (see O'Brien and Van Wyk, 1984, for review). Brinkmann (1936) observed slower growth of a cohort of galatheids parasitized by a lernaeodiscid rhizocephalan than the unparasitized cohort. In the rhizocephalan family Peltogastridae (Bourdon, 1963)

and perhaps the Lernaeodiscidae (Veillet, 1945), a positive correlation between host size and parasite prevalence has been observed: a pattern that is frequently associated with parasitic castrators (Kuris, 1974; Baudoin, 1975; Kuris *et al.,* 1980).

The existence of other interactions between rhizocephalans and their hosts, while not necessarily precluding precocious maturity, may mask it and make precocious maturity difficult to detect. Alternatively, it can be questioned whether precocious maturity actually is the appearance of adult structures early in development, as the term 'precocious' implies, if the only evidence is a smaller size of parasitized adult hosts. Many causes of size differences among groups of crustaceans have been reported: differential growth (Kinne, 1959; Newman and Pollock, 1974), size selective predation (Brooks and Dobson, 1965), and season of maturation (Kuris, 1971) to name just a few. Yet, other than documenting size differences between parasitized and unparasitized crabs, no study has provided evidence that infection by a sacculind actually resulted in the precocious acquisition of the adult morphology by the host.

This study demonstrated causal factors leading to smaller adult mean size of the majid crab, *Pugettia producta,* parasitized by the sacculinid, *Heterosaccus californicus.* Infection did not alter molt increments from those of unparasitized animals, but did reduce the number of molts before the molt of puberty. This is the first study to document with laboratory and field evidence precocious maturity in hosts parasitized by Rhizocephala.

Materials and Methods

Pugettia producta individuals were collected monthly from Coal Oil Point, Goleta, Santa Barbara County, California from November 1976 to September 1982. Crab carapace length was measured to the nearest 0.1 mm from the tip of the rostrum to the midline of the posterior carapace margin. Sexual maturity of the crabs was determined from allometric changes of the male chela and from female abdominal width associated with the molt of puberty (Pérez, 1928; Hartnoll, 1967; O'Brien, in prep). Crabs were individually marked using the position of holes punched in the exoskeleton (Born, 1970; Kuris, 1971). Adult crabs were recorded as parasitized if they possessed either the external stage (externa) of the rhizocephalan or a necrotic scar on the abdomen where the externa had detached from the host (Lützen, 1981). All crabs with a compressible merus and parasitized crabs with externa lacking a mantle opening were assumed to have matured in the month of collection. The population structure of adult crabs was determined from records of first capture only.

Laboratory growth studies were conducted at the Marine Laboratory of the University of California, Santa Barbara. Crabs were maintained individually in 0.5 to 2.25 liter perforated polyethylene freezer containers depending on size of crab. The containers were submerged in ambient flowing sea water. Crabs were inspected daily and fed the kelp, *Egregia laevigata.* Only first laboratory molts of crabs of comparable size missing no more than one leg were used in the statistical analyses. In an experiment designed to determine if there was a difference in the number of molts to maturity between parasitized and unparasitized crabs, a cohort of crabs was maintained through two laboratory molts. To minimize variability, all crabs in this experiment were collected at the same time (one tidal series in May 1979) at the same place (Coal Oil Point) from the same alga (*E. laevigata*) and were of similar size (29.5–34.7 mm). Consecutive instars of these crabs were counted until the parasitized crabs matured. Statistical analyses were conducted according to Sokal and Rohlf (1981), except for separation of modes by probability graph paper (Cassie, 1954). Unbalanced two-way ANOVA and Duncan multiple range tests were computed by the UCSB ITEL AS/ 6 computer using Statistical Analysis System (SAS) (Helwig and Council, 1979).

Comparisons of linear regressions were done by ANCOVA based on a program from Zar (1974).

RESULTS

Host size distribution

No parasitized host was found larger than 85 mm. Only 0.4% of the parasitized population (3 crabs) was larger than 80 mm, although 11.7% of the unparasitized adult population exceeded this size (Fig. 1). Mean size of parasitized adults [59.2 mm ± 7.8 (S.D.) (n = 730)] was significantly less than the respective mean sizes of unparasitized adult females and males [66.5 mm ± 9.4 (n = 1846) and 67.8 ± 12.6 (n = 1615)] ($P < 0.001$, Student's t-test).

Using probability graph paper the size frequency distribution of parasitized adult crabs was separated into three modes. The first mode had a mean of 56 mm and comprised 62% of the parasitized population. Succeeding modes had means of 67 and 79 mm constituting 35% and 3% of the population respectively. Percentage of hosts parasitized (prevalence) within the total adult population was 17.4%. Prevalence decreased with increasing host size above a carapace length of 57 mm (Table I). Almost 90% of the parasitized population was found between 46 and 69 mm carapace length (Table I).

Molt increment

Linear regressions of molt increments (post-molt length − pre-molt length) of immature crabs as a function of pre-molt carapace lengths were: parasitized crabs ($Y = 0.283x + 1.255$, $r = 0.876$, $n = 22$), unparasitized females ($Y = 0.356x − 0.854$, $r = 0.939$, $n = 75$) and unparasitized males ($Y = 0.293x + 0.333$, $r = 0.922$, $n = 65$). When subjected to ANCOVA at $P = 0.05$, no significant difference between these regressions in slope or elevation was found whether parasitized crabs were
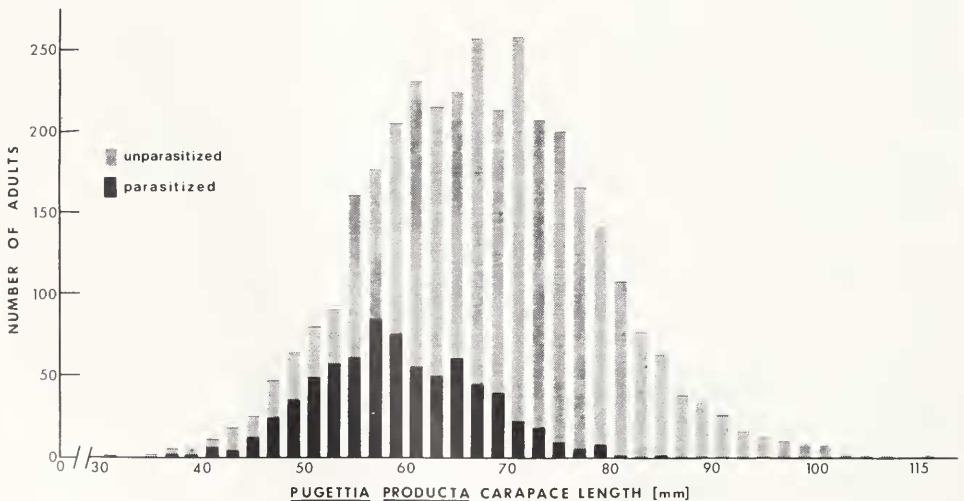

FIGURE 1. Size-frequency distribution of unparasitized *P. producta* adults and adults parasitized by *H. californicus*. Data were collected from Coal Oil Point from 1975–1982. Values for parasitized animals are superimposed upon those of unparasitized animals.

TABLE I

Prevalence (%) and size-frequency distribution of adult H. californicus *within size-classes of the adult* P. producta *population at Coal Oil Point California*

Host carapace length (mm)	<45	46–57	58–69	70–81	82–93	>94
Percent of *P. producta* parasitized (n = 4,186)	27.2	31.7	19.6	5.5	0.8	0.0
Percent of *H. californicus* population (n = 729)	3.4	42.7	45.0	8.6	0.3	0.0

compared with unparasitized females (Fig. 2) (slope F = 2.88, y-intercept F = 0.421) or unparasitized males (slope F = 0.375, y-intercept F = −3.151).

The linear regression which was computed for molt increments at the molt of puberty against carapace length for parasitized crabs was significant (Fig. 3) (r = 0.603, critical value at P = 0.01 was r = 0.575). However, if the data point for the largest parasitized crab (54.3, 18.0) was omitted from the computation, the correlation of the resulting linear regression (r = 0.392) was not significantly different from r = 0. The comparable regressions for unparasitized females (r = 0.37) and unparasitized males (r = 0.021) were also not significantly correlated. Molt increment at the molt of puberty was not correlated with pre-molt size. Comparing all observed increments
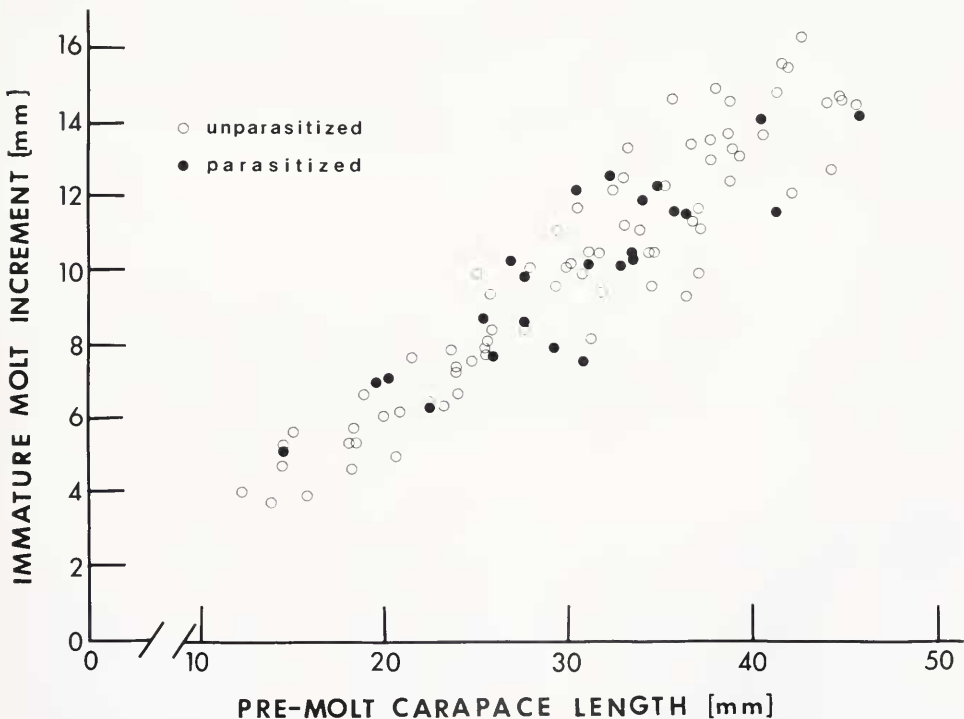

FIGURE 2. Increase in size at the first laboratory molt for parasitized juvenile female *P. producta* and of juveniles parasitized by *H. californicus* as a function of pre-molt carapace length.
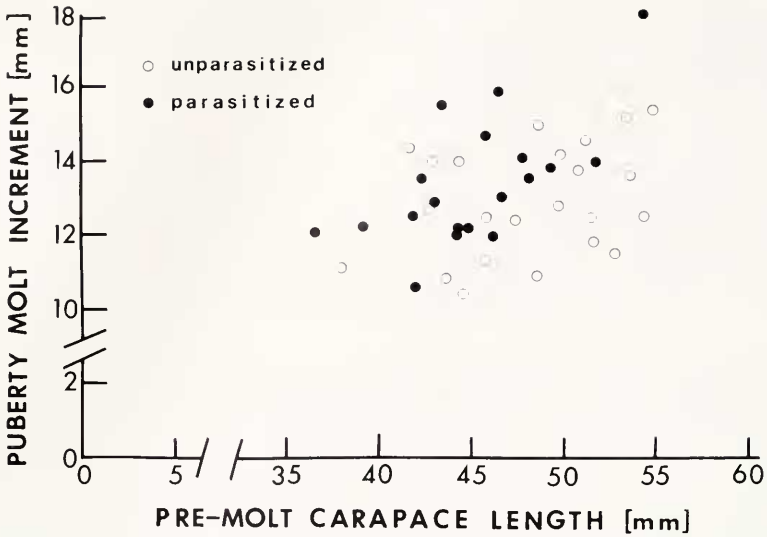
FIGURE 3. Increase in size at the molt of puberty for unparasitized female *P. producta* and of individuals parasitized by *H. californicus* as a function of pre-molt carapace length.

at the molt of puberty using the Mann-Whitney U-test revealed no significant difference between parasitized and unparasitized females ($P > 0.20$) nor between parasitized and unparasitized male crabs ($P > 0.10$). Linear regressions of log-log transformations of pubertal molt increments were also determined for unparasitized females ($y = 0.4693x + 0.321$; $r = 0.365$) and parasitized crabs ($y = 0.7903 - 0.1844$; $r = 0.578$). ANCOVA revealed no significant difference between slopes ($0.50 > P > 0.25$, $F = 0.698$) nor intercepts ($0.10 > P > 0.05$, $F = 3.301$) of the linear regressions of the transformed data.

Number of molts to maturity

The first laboratory molt of the entire cohort of parasitized and unparasitized crabs was an immature molt. Of those individuals molting a second time, a significantly greater proportion of parasitized crabs underwent the molt of puberty than of unparasitized crabs. ($P = 0.005$, G-test of independence) (Table II).

TABLE II

Maturation state of similar-sized P. producta *following a second laboratory molt*

	Number of adults	Mean length (mm) Pre-molt	Mean length (mm) Post-molt	Number of juveniles	Mean length (mm) Pre-molt	Mean length (mm) Post-molt
Parasitized	5	43.8 ± 3.38*	53.3 ± 2.42	1	43.7	56.0
Unparasitized	1	47.7	56.3	10	42.1 ± 1.79	50.5 ± 3.24

* = Student's *t*-interval, $P = 0.05$.

Instar duration

Instar durations of unparasitized male and female crabs undergoing immature molts were not significantly different ($P > 0.40$, Mann-Whitney U-test) nor did they differ significantly from instar durations of parasitized crabs (Fig. 4) ($P > 0.30$, Mann-Whitney U-test). Similar comparisons of instar durations preceding molts of puberty revealed no significant differences between unparasitized males and females nor between parasitized and unparasitized crabs ($P > 0.10$).

Maturation season

About 90% of the molts of puberty observed in the field and laboratory occurred during the period from May through October, the maturation season (Fig. 5). Throughout the maturation season when a parasitized crab larger than 30 mm molted, it was much more likely to undergo the molt of puberty than a concurrently molting unparasitized crab. Thus, the relative frequency of pubertal molts (total number of pubertal molts divided by the number of all observed molts $\times$ 100) for crabs larger than 30 mm was significantly greater for parasitized than unparasitized crabs ($P < 0.001$, G-test of independence) (Fig. 6). In addition, size at maturity was strongly correlated with both the presence of a parasite ($F = 23.54$, $P < 0.0001$) and month in which maturation occurred ($F = 3.93$ $P < 0.01$, ANOVA) (Table III). Furthermore, as the maturation season progressed there was a significant difference in how mean size at maturity changed over time, decreasing for parasitized while increasing for unparasitized crabs ($P < 0.006$, $F = 4.39$, ANOVA). Analysis by the *a posteriori* Duncan's multiple range test at $P = 0.05$ revealed no significant differences in size at maturation for parasitized and unparasitized crabs maturing in May and June, but during the periods July–August and September–October mean size of newly
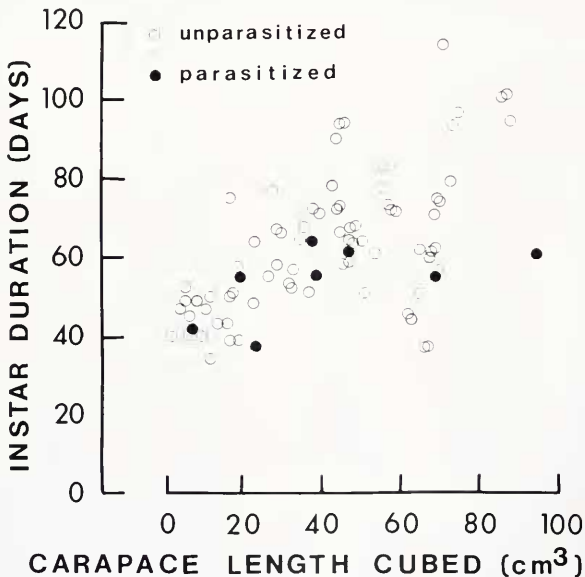

FIGURE 4. Instar duration of unparasitized juvenile *P. producta* and of juveniles parasitized by *H. californicus* plotted as a function of the cube of the pre-molt carapace length.
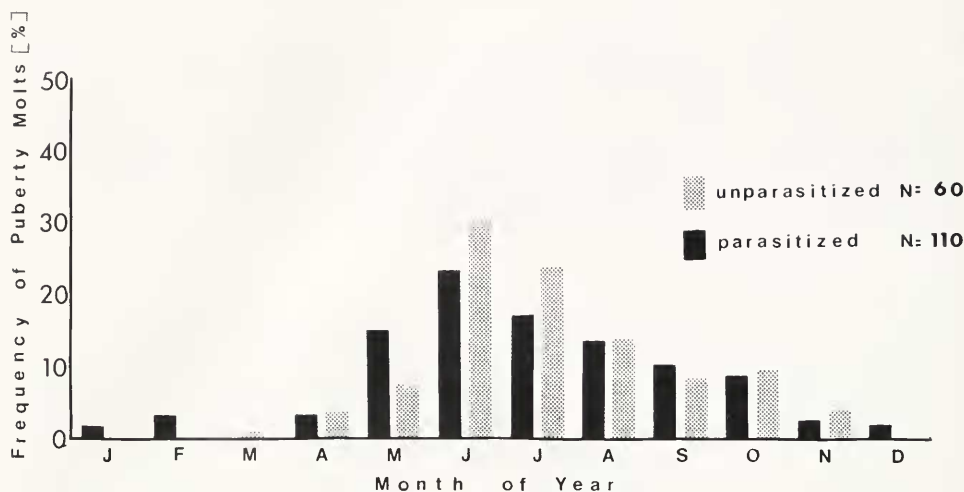
FIGURE 5. Relative frequency of molts of puberty from 1975–1982 computed as a percentage of the total number of puberty molts observed (N). Monthly values were computed independently for unparasitized *P. producta* and for crabs parasitized by *H. californicus*. Data were from monthly samples from Coal Oil Point.

matured parasitized crabs was significantly less than that of unparasitized crabs (Table III).

DISCUSSION

Prevalence of the rhizocephalan parasite, *Heterosaccus californicus*, was negatively correlated with increasing host size (Table I). No large adult crabs (>85 mm) were
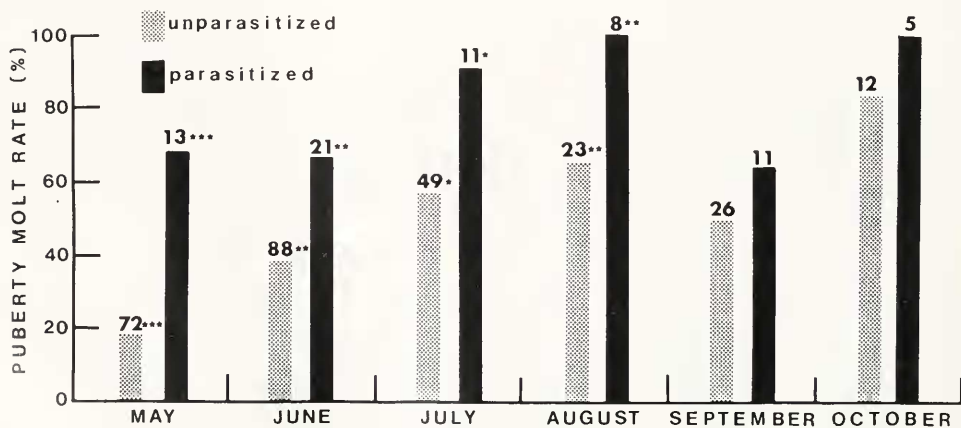

FIGURE 6. Relative rate of molts of puberty (total number of molts of puberty divided by total of all molts times 100) for crabs greater than 30 mm pre-molt carapace length. Numbers above each column indicate total number of molts observed for that crab group in that month. Data were accumulated from 1975 to 1982. Asterisks indicate significant differences between within month values at the following levels: ***$P < 0.001$, **$P < 0.025$, *$P < 0.05$, and lack of an asterisk indicates $P > 0.05$ (G-test of independence).

TABLE III

Size at maturity of parasitized and unparasitized P. producta *by months in which maturation occurred*

	Month	May–June	July–August	September–October
Unparasitized	n	44	42	19
	Size-range	50.1–77.2	54.3–86.2	54.8–94.9
	Mean size (mm CL)	62.8 ± 2.12*	65.0 ± 2.89	67.2 ± 4.29
Parasitized	n	23	18	11
	Size-range	51.4–78.7	38.8–63.0	50.5–62.0
	Mean size (mm CL)	60.7 ± 2.68	52.4 ± 3.08	57.9 ± 2.83

* = Student's *t*-interval, $P = 0.05$.

parasitized. However, the lower size limits of both parasitized and unparasitized adults were similar (Fig. 1). This study considered five possible explanations: 1) higher mortality of large parasitized crabs, 2) differential growth of parasitized and unparasitized adults, 3) differential growth of parasitized and unparasitized juveniles, 4) an environmental factor independent of the parasite, and 5) precocious maturity of parasitized hosts for the observed size differences between parasitized and unparasitized crabs.

A mortality rate of large parasitized crabs greater than that of unparasitized crabs seemed an unreasonable explanation for the observed size differences because no large (>85 mm) parasitized crabs were ever found. Sampling was conducted monthly for seven years and if significant numbers of large parasitized crabs had matured, some probably would have been detected, even if they had died shortly after maturation. In addition, parasitized crabs matured in the laboratory over the same size range as those found in the field; the largest newly matured parasitized crab (78 mm) was almost as large as the largest parasitized crab collected (85 mm). Both laboratory and field evidence corroborated on a maximum size of adult parasitized crabs which was about 20% (20–25 mm) less than the maximum size of unparasitized crabs.

Differential growth of adult crabs was rejected as an explanation for the observed size differences because most majid crabs including, *P. producta,* do not molt after the molt of puberty (Tessier, 1935; Carlisle, 1957; Hartnoll, 1963; Born, 1970). The smaller size of parasitized crabs must have resulted from events that occurred during the juvenile growth phase.

Two workers have examined the effect of sacculinids upon growth of juvenile crabs. Veillet (1945) concluded that the smaller size of *C. maenas* parasitized by *Sacculina carcini* was caused in part by reduction of the molt increment of large juvenile crabs. Veillet observed no difference between molt increments of small parasitized and unparasitized juveniles but did note a difference in larger sizes. Since the energy demands of adult rhizocephalans might sufficiently drain the host's lipid reserves and negatively affect host growth (Smith, 1906), Veillet theorized that immediately following infection *S. carcini* was too small to influence host growth. Veillet suggested that as the parasite grew it exerted an increasingly negative effect upon host growth; thus, only large parasitized juveniles displayed relatively small molt increments. In contrast Vernet-Cornubert (1958) concluded infection by *S. carcini* had no overall effect on the molt increments of *Pachygrapsus marmoratus.* However, a few extremely feminized male *P. marmoratus* did have relatively small molt increments. In the present study, infection of *Pugettia producta* by *H. californicus* had no significant

effect on molt increments of immature molts (Fig. 2) nor molts of puberty (Fig. 3). These molt increment values also agreed well with those measured by Born (1970) and Hines (pers. comm.) for unparasitized *P. producta*. The molt of puberty for *P. producta* was the terminal ecdysis, during which the parasite would have been most developed and presumably would have been making the largest energy demands upon the host. The lack of a significant difference between increments of immature molts at the molt of puberty coupled with no observed differences in instar duration between parasitized and unparasitized crabs (Fig. 4) justified excluding differential juvenile growth as an explanation of *P. producta* size differences.

The size of parasitized crabs could have been determined by an environmental factor and not the parasite. If season of recruitment or algal substrate (food) influenced *Pugettia* size and if *Heterosaccus* larvae were seasonal or restricted spatially within the habitat, it was possible that only crabs that were going to be small adults had been exposed to infection. Because no difference was detected in instar duration (Fig. 4), I assumed that similar-sized parasitized and unparasitized crabs had recruited concurrently. By following growth of similar-sized parasitized and unparasitized crabs from the same microhabitat, a mutually exclusive experiment was conducted. If all the crabs had been observed to pass through the same number of instars before maturing, the existence of an independent factor determining parasitized host size would have been supported. However, parasitized crabs underwent significantly fewer ecdyses before maturation (Table II). This result supported the precocious maturity explanation while rejecting differences in spatial or temporal variability of parasitization as the cause of differential size. Field data also supported the precocious maturity explanation. Parasitized crabs were found undergoing molts of puberty in far greater relative numbers than unparasitized crabs at the beginning of the maturation season (Fig. 6). In May 70% of parasitized crabs above 30 mm carapace length molted to maturity when they molted, a level not attained by the unparasitized population until 3 months later. Consequently, the simplest explanation for the smaller adult size of parasitized *P. producta* was that parasitized crabs passed through fewer instars before the molt of puberty.

Previous explanations of variation in adult size of *Pugettia*, readily incorporated the effect of the rhizocephalan on *Pugettia* size. Born (1970) felt that the broad size range of adult *P. producta* was a result of recruitment through the year with seasonal maturation. Crabs that did not mature one season would continue to grow and become the largest crabs a year later. Kuris (1971) working with the shore crab, *Hemigrapsus oregonensis*, broadened the model, postulating a size-threshold above which size juvenile crabs would undergo the molt of puberty. The size-threshold could vary during the year. Seasonality of the molt of puberty resulted from a seasonal decrease in this size-threshold. Crabs within size-classes between the two thresholds complete the molt of puberty after the threshold falls. Kuris (1971) did not state which conditions might cause such a decrease, but suggested that a seasonal increase in the size-threshold for maturation might be adaptive. Relatively small *H. oregonensis* matured at a time (the winter) when growth conditions were poor but reproduction was high. Inclusion of a stochastic element into the Born-Kuris model can explain the observation (Hartnoll, 1963, p. 451; Born, 1970; O'Brien, this paper, Table II) that not all majid crabs pass through the molt of puberty together even if they are the same size and are molting concurrently. Since not all crabs larger than the size-threshold undergo the molt of puberty at the very next ecdysis, I suggest that it is the probability of undergoing the molt of puberty that increases with crab size.

The essentials of the size-threshold model were supported by the data from the Coal Oil Point population. Precocious maturity can be explained as a greater sensitivity of parasitized crabs to the stimuli that induce maturation above the size-threshold.

Since the minimum sizes of parasitized and unparasitized *Pugettia* were equivalent (Fig. 1), the value of the size-threshold was not affected by the rhizocephalan. In fact, early in the maturation season (May and June), the mean size of newly matured animals did not differ between parasitized and unparasitized crabs (Table III). The size-threshold of maturation appeared to have suddenly lowered before May and June at Coal Oil Point (Fig. 7C, D). Less than half of the unparasitized juveniles that molted during the early maturation season (May and June) underwent a molt of puberty (Fig. 6), thus, mean size of the cohort of unparasitized juveniles continued to increase to the middle of the maturation season (July and August) (Fig. 7E). While small unparasitized adults matured throughout the maturation season as shown by the equivalence of the lower size-ranges, the upper range and mean size steadily increased which meant that large adults appeared during the middle and late maturation season (July through October) (Table III, Figs. 7E, G).
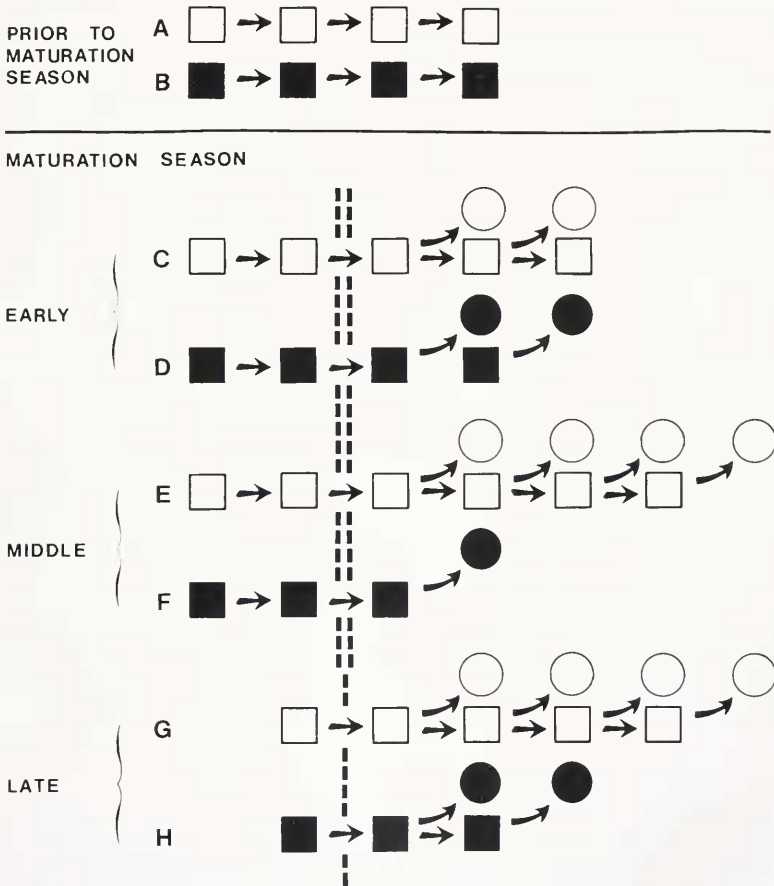

FIGURE 7. Schematic representation of a model explaining differences in adult size between unparasitized *P. producta* and those parasitized by *H. californicus* based on the Born-Kuris size-threshold model. Representations are as follows: circles = adult crabs, squares = juvenile crabs, diagonal arrows = molts of puberty, and horizontal arrows = immature molts. Absence of arrows between symbols indicates individuals are not passing through those particular instars at that time. Size increases from left to right with vertically aligned symbols representing individuals of equivalent size. The position and number of the broken lines indicate initial size and relative intensity of the size-threshold effect. See text for details.

The timing of maturation of parasitized hosts was much different than that of unparasitized crabs. A significantly higher percentage of parasitized juveniles that molted in May and June underwent the molt of puberty than did unparasitized juveniles (Fig. 6). In other words, few parasitized crabs above the size-threshold underwent immature molts (Fig. 7D) while large numbers of unparasitized juveniles continued to do so (Fig. 7C). There was no significant difference between mean size of newly matured parasitized and unparasitized crabs in May and June (Table III), because equivalent growth rates of juveniles (Figs. 2, 3, and 4) resulted in equivalent size of the juvenile cohorts from which the adults arose (Figs. 7A, B, C, and D). However, the lack of immature molts by parasitized juveniles early in the maturation season implied that the cohort of parasitized juveniles did not increase in size (Fig. 7F) and, consequently, there were no new mature hosts larger than 63 mm in the middle of the maturation season (July and August) (Table III). Parasitized hosts underwent the molt of puberty immediately following attainment of the size-threshold as evidenced by the relative pubertal molt rate close to 100% (Fig. 6). This explains why the smallest mode of parasitized *P. producta* contained more animals than modes in the larger parasitized size-classes (Fig. 1).

The conditions that induced the molt of puberty appeared to wane in the later maturation season (September and October). The pubertal molt rate for parasitized crabs decreased in September (Fig. 6) and mean size of newly matured parasitized hosts increased slightly, but still remained significantly less than mean size of unparasitized animals (Table III, Figs. 7G, H). Events late in the maturation season did not influence population structure of parasitized hosts as much as earlier maturations because the number of crabs maturing during this time was relatively low (Fig. 5). It was the cessation of the immature growth phase by parasitized crabs in the middle months of the maturation season (Fig. 7F) that resulted in the smaller mean size of *P. producta* parasitized by *H. californicus.*

In the *Heterosaccus-Pugettia* system, laboratory observations did not detect any differences between the two most commonly measured parameters of crustacean growth, molt increment, and instar duration. Instead, field observations and the laboratory growth experiment supported an explanation of precocious maturity for the observed differences in size between parasitized and unparasitized adults. The average parasitized adult crab passed through fewer instars than the average unparasitized adult. Thus, the difference in size between two groups of crabs was not attributable to a difference in the growth rate, but to a difference in the duration of the juvenile growth phase. Variation in the number of juvenile instars is probably not limited to parasitic castrator-crustacean host systems, rather such variation is simply more easily observed within such systems. Any thorough investigation into the causes of size differences among groups of adult crustaceans must consider variation in the number of juvenile instars as one of the reasonable explanations to be tested.

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